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Scale microstructure and its phylogenetic implications in lycaenid butterflies (Lepidoptera, Lycaenidae)*

R. J. D. TILLEY[1] and J. N. ELIOT[2]

[1]1 The Paddocks, Lower Penarth, South Glamorgan CF64 5BW, UK
[2]Upcott House, Bishop's Hull, Taunton TA4 1AQ, UK

Abstract The structural scales that give rise to the characteristically vivid green, blue or violet iridescent colours of some 47 species of Lycaenidae and 7 species of Riodinidae have been examined by optical and scanning electron microscopy. Most species of Lycaenidae examined produce iridescent colours via a multilayer elaboration within the lumen of the scale into a *Urania*-type microstructure. The multilayers were found to be perforated and possess a characteristically complex and typical microstructure, referred to as a pepper-pot structure. In addition, colour production by a *Morpho*-type structure was unexpectedly found in some species of the subfamily Lycaeninae. This microstructure results from an elaboration of flutes on the ridges and is quite distinct from *Morpho*-type scales found in the Riodinidae, which are derived from scutes. The phylogenetic and taxonomic usefulness of scale microstructure is considered and it is speculated that within Lycaeninae *Morpho*-type scales may have evolved by transition from *Urania*-type scales.

Key words Scales, ridges, trabeculae, flutes, scutes, *Urania*-type, *Morpho*-type, pepper-pot structure, Lycaenidae, Riodinidae.

Introduction

The flattened blade of a generic or undifferentiated scale on the wings of a butterfly consists of a virtually featureless reverse surface and an obverse surface which appears to consist of open cells formed by longitudinal ridges and cross ribs to form a set of roughly rectangular "windows" through which the reverse surface is visible. The cross ribs are joined to the lower lamella by trabeculae (Downey & Allyn, 1975; Ghiradella, 1989). The ridges bear flutes on their sides, and are topped by an overlapping series of narrow and elongated laminae termed scutes by Downey & Allyn and ridge lamellae by Ghiradella. Henceforth we use the former term. Scales with this structure are present over much of the wing surfaces and are usually coloured by pigments.

The vivid colours, normally ranging across the blues and violets, but extending into the ultraviolet and greens, of the upper wings of many Lycaenidae, arise from microstructural developments of the undifferentiated structure in essentially transparent scales. These changes cause the components of white light falling upon the scales to interfere one with another; the resulting reflected colour being due to physical effects and not pigmentation (Onslow, 1921; Mason, 1926, 1927). Two microstructures were singled out by Mason (1927) as being of greatest importance in colour production. In the first, the origin of the colour was generally regarded as being due to multiple layers of material occurring between the obverse and the reverse surface of the scale. This type of arrangement has been referred to as the *Urania*-type, having initially been described from optical microscope observations of

*Correspondence to J. N. Eliot.

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Urania ripheus [recte *Chrysiridia rhipheus*] (Mason, 1927). The second was suggested after examination of *Morpho menelaus* (Mason, 1927). In this and related insects, the colour is produced by the structure of the longitudinal ridges and the scales are known as *Morpho*-type. Both types are subject to considerable modification, which we discuss further later. In both *Urania*- and *Morpho*-type scales the colour perceived is usually greatly enhanced by a layer of darkly pigmented basal scales lying under the iridescent scales. These absorb any light that passes through the transparent iridescent scales without reflection and significantly strengthen the perception of the iridescent effect.

The most extensive studies of butterfly scale morphology have been made by Ghiradella (1984, 1985, 1989, 1991, 1994, 1998). This impressive body of work has mainly focussed upon the Papilionidae, and relatively few examples of lycaenid scales are featured. Other studies of the microstructures of the iridescent scales of lycaenid butterflies have been sporadic, most mentioning only one or two species (Gentil, 1959; Sellier, 1971; Morris, 1975; Allyn & Downey, 1975; Downey & Allyn, 1975; Meyer-Rochow & Eguchi, 1983; Meyer-Rochow, 1991). An exception is the study of 21 Palaearctic Lycaenidae by Schmidt & Paulus, 1970). These studies have led to the belief that iridescent colour production in Lycaenidae is inherently due to *Urania*-type scale microstructures. However, in these insects the featureless multiple layers characteristic of the classical *Urania*-type are replaced by layers that are perforated to a greater or lesser extent to produce rather complex microstructures. This feature, typical of the Lycaenidae, has been termed a "pepper-pot" structure by Eliot (1973) and referred to as plebeid-type by Downey & Allyn (1975). When necessary to stress this feature we refer to *Urania* (pepper-pot)-type scales.

In the present study, we have examined a cross-section of butterflies from the four subfamilies of Lycaenidae and added several examples from the Riodinidae for comparison. The broad aim was to determine if a study of scale morphology would be of utility from a phylogenetic or taxonomic point of view. The results are presented in this paper.

Materials and methods

The butterflies listed in Table 1 were wild caught insects, mainly (but not entirely), from South-East Asia and Western Europe. The observations focus upon the scales which characterise the insects studied and which produce colour mainly by structural effects.

All specimens were initially examined optically using a Meiji microscope and this was used to select scales for electron microscope examination. Some specimens were illuminated with ultraviolet light in order to check for iridescence below the visible spectrum, as noted in Table 1. For this, a Spectraline E series ultraviolet lamp (Spectronics Corp.) was used to illuminate the insects. Images were observed with a Swift TV camera (Custom Cameras Ltd) having a wavelength sensitivity down to 350 nm and a resolution of 700 TV lines. The image was displayed on a monochrome high resolution TV monitor. A Schott glass UG1 ultraviolet filter (Comar Instruments) which had a transmission peak at 360 nm and was opaque to visible light was inserted in front of the TV camera to eliminate visible light. The iridescent reflection of ultraviolet light was typically very angular dependent and it was necessary to tilt each butterfly over considerable angles to be sure of seeing the effect. This angular dependence is not noted in Table 1. If no mention of ultraviolet reflectivity is made, the insect was not examined in this way.

To determine the microstructure of scales, whole wings or fractured individual scales were examined by scanning electron microscopy. In the latter case, the selected scales were gently

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removed from the wings using a fine sable-hair brush, dusted onto an aluminium "stub" and cooled in liquid nitrogen. Cold scales were fractured using a fine needle under observation in an optical microscope. Note that such cooling is needed to make the scales brittle enough to fracture. (At room temperature the scales are simply squashed flat by the needle.) Both the whole wings and the fractured scales were gold coated and examined by scanning electron microscopy using a Jeol 35CF or a Hitachi S570 microscope, both operated at 30 or 35 kV voltage and at magnifications up to 30,000×.

Sections of some scales were examined by transmission electron microscopy. Scales were selected optically and placed with a fine sable hair brush into a silicone rubber mould. The moulds were then filled with Spurr resin that was polymerised by curing at 60°C for 24 hr. The resin was removed from the mould and sectioned with an LKB Ultratome III microtome. Sections were stained with 1% potassium permanganate in a pH 6 phosphate buffer and examined with a Jeol 1210 transmission electron microscope operated at 80 kV.

Results

The results for the species of Lycaenidae examined are presented in summary form in Table 1, and what follows is an expansion of detail for selected species. In Table 1, the taxonomic arrangement follows that proposed by Scott & Wright (1990) and also by Fiedler (1991) but we have chosen to regard the subfamily Riodininae as a distinct family in accordance with current American practice (Harvey, 1987; Robbins, 1988; DeVries, 1997; Ghiradella, 1998). The small number of Riodinidae examined, for comparative purposes, is listed in Table 2.

The scales giving rise to the major structural coloration of the insect are illustrated in Figs 1–14 in the same order as in Tables 1 and 2. In the main, these are flat scales similar in overall shape to the undifferentiated form. It is necessary to stress, though, that there is considerable variation in the exact microstructure of these scales, both between the apical and basal region of an individual scale and in scales from different areas on the wings. Our illustrations are representative of the microstructures observed and do not show every variation found. Apart from flat scales, many species also possess regions densely covered with piliform scales (Downey & Allyn, 1975), or bristles (Ghiradella, 1998). These features, often loosely called "hairs", are homolgous to flat scales, and contribute to the overall appearance of the wing. These have not been specifically illustrated except for several cases of particular interest, as described below.

Apart from a list of the species examined, Table 1 contains some additional information about the scales studied. The entry for the colour of the scales simply records subjective impressions of the colours of the scales examined in daylight in order to allow the reader to identify the scales involved, and is not meant to be a quantitative assessment of colour. The colour is followed by a note of the ultraviolet reflectivity of the whole wing, where known, reported as strong, medium, weak or nil. The ultraviolet reflectivity is included to give an overall impression of the wing contrast that may be perceived by an insect. The structural scale morphology is described as *Urania*-type, when colour is generated by multilayers of a pepper-pot structure, or *Morpho*-type, when the colour is generated by a development of the ridges. The ridges on the scales examined are roughly characterised by the height (low, moderate or deep), followed by their average spacing. The term "undifferentiated" in Table 1 means that no obvious *Urania*- or *Morpho*-type microstructure was seen.

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Table 1. Species of Lycaenidae examined.

subfamily tribe subtribe species	sex colour*	scale type**	ridge type*** (length in μm)
Poritiinae			
Poritiini			
Poritia sumatrae (C. & R. Felder, 1865)	♂ turquoise-blue	*Urania*-type	low; ~1.25
Miletinae			
Miletini			
Allotinus subviolaceus C. & R. Felder, 1865	♀ pale matt-blue; strong	undiff	moderate; ~1.4
Curetinae			
Curetis bulis stigmata (Moore, 1879)	♂ shining copper-orange	undiff	moderate; ~1.15
Lycaeninae			
Aphnaeini			
Spindasis syama (Horsfield, 1829)	♂ brownish[1], strong[2]	*Morpho*-type	deep; ~0.6
Spindasis nipalicus (Moore, 1884)	♂ deep violet-blue	*Morpho*-type	deep; ~0.7
Poecilmitis chrysaor (Trimen, 1864)	♂ shining orange, nil	undiff	deep; ~1.4
Eumaeini			
Deudorigina			
Rapala rhoecus de Nicéville, 1895	♂ deep violet-blue; strong	*Morpho*-type	deep; ~0.9
Rapala manea (Hewitson, 1863)	♂ brownish[1], strong	*Morpho*-type	deep; ~0.7
Rapala pheritima (Hewitson, 1863)	♀ shining indigo-blue	undiff	moderate; ~2.1
Artipe eryx (Linnaeus, 1771)	♂ deep turquoise-blue	*Morpho*-type	deep; ~0.8
Sithon nedymond (Cramer, 1780)	♂ deep violet-blue	*Morpho*-type	deep; ~0.7
Tomarina			
Tomares ballus (Fabricius, 1787)	♂ green[3]	*Urania*-type[4]	
Eumaeina			
Siderus tephraeus (Geyer, 1837)	♂ cobalt blue; weak	*Urania*-type	deep; ~2.1
Eumaeus minijas (Hübner, 1809)	♂ turquoise; nil	*Urania*-type	deep; ~2.3
Atlides halesus (Cramer, 1777)	♀ green-blue; strong	*Urania*-type	moderate; ~2.0
Arawacus meliboeus (Fabricius, 1793)	♂ pale blue, strong	*Urania*-type	moderate; ~1.5
Callophrys rubi (Linnaeus, 1758)	♂ green[4], nil	*Urania*-type	moderate, ~1.5
Callophrys avis Chapman, 1909	♂ green[4]	*Urania*-type	moderate, ~1.5
Hypolycaenina			
Hypolycaena erylus (Godart, 1824)	♂ deep blue-violet; strong	*Morpho*-type	deep; ~0.5
Chliaria othona (Hewitson, 1865)	♂ bright sky-blue	*Urania*-type	deep; ~1.4
Catapaecilmatina			
Catapaecilma major H. H. Druce, 1895	♂ violet-blue	*Urania*-type	low; ~1.6
Loxurina			
Drina maneia (Hewitson, 1863)	♂ deep blue	*Urania*-type	moderate; ~1.55
Horagina			
Horaga syrinx (C. Felder, 1860)	♂ shining pale sky-blue	*Urania*-type	moderate; ~1.55
Cheritrina			
Drupadia ravindra (Horsfield, 1828)	♂ shining sky blue	*Urania*-type	moderate; ~1.85
Amblypodiina			
Iraota rochana (Horsfield, 1829)	♂ shining turquoise; strong	*Urania*-type	low; ~1.9
Iolaina			
Tajuria cippus (Fabricius, 1798)	♂ shining blue; strong	*Urania*-type	low; ~2.0
Remelanina			
Remelana jangala (Horsfield, 1829)	♂ deep violet-blue	*Urania*-type	low; ~1.4
Ancema blanka (de Nicéville, 1894)	♂ bright shining blue	*Urania*-type	low; ~1.8
Theclini			
Theclina			
Quercusia quercus (Linnaeus, 1758)	♂ purple, strong	*Urania*-type	low; ~1.7
Laeosopis evippus (Hübner, 1793)	♂ purple, strong	*Urania*-type	low; ~2.2
Arhopalina			
Arhopala pseudocentaurus (Doubleday, 1847)	♂ deep blue; strong	*Urania*-type	low; ~2.7

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Arhopala aurea (Hewitson, 1862)	♂ shining gold-green; nil	*Urania*-type	low; ~2.5
Arhopala eumolphus (Cramer, 1780)	♂ shining gold-green; nil	*Urania*-type	low; ~2.7
Surendra florimel Doherty, 1889	♂ deep blue	*Urania*-type	low; ~2.0
Surendra vivarna amisena (Hewitson, 1862)	♂ deep blue	*Urania*-type	low; ~2.4
Lycaenini			
Lycaena virgaureae (Linnaeus, 1758)	♂ shining orange, strong	undiff	moderate, ~0.9
Lycaena alciphron (Rottemburg, 1775)	♂ purple, strong	*Urania*-type	moderate, ~2.1
Heliophorus androcles (Westwood, 1852)	♂ deep sky blue; medium	*Urania*-type	low; ~1.2
Polyommatini			
Lycaenesthina			
Anthene lycaenina (R. Felder, 1868)	♂ shining violet blue; strong	*Urania*-type	moderate, ~2.0
Candalidina			
Candalides margarita (Semper, 1879)	♂ dull indigo; strong	*Urania*-type	moderate, ~2.0
Niphandina			
Niphanda tesselata Moore, 1875	♂ deep blue-indigo; strong	*Urania*-type	low; ~2.0
Polyommatina			
Jamides caeruleus (H. Druce, 1873)	♂ shining sky-blue; strong	*Urania*-type	moderate, ~1.8
Celastrina argiolus (Linnaeus, 1758)	♂ blue; strong	*Urania*-type	moderate, ~1.8
Cupido minimus (Fuessly, 1775)	♂ blue scale	*Urania*-type	moderate, ~1.5
Glaucopsyche alexis (Poda, 1761)	♂ blue	*Urania*-type	moderate, ~1.2
Polyommatus escheri Hübner, 1823	♂ sky blue	*Urania*-type	moderate, ~1.3
Polyommatus daphnis ([Denis & Schiffermüller], 1775)	♂ pale blue	*Urania*-type	moderate, ~1.5
Polyommatus coridon (Poda, 1761)	♂ silvery blue	*Urania*-type	moderate, ~1.3

Notes.

* The colour is that of the scales investigated, seen in daylight, followed by the ultraviolet reflectivity of the whole wing, where known, reported as strong, medium, weak or nil.

** The scales are defined as undifferentiated (undiff), *Urania* (pepper-pot)-type and *Morpho*-type.

*** The ridges are defined by the height above the visible membrane, followed by the average spacing of the ridges.

[1] The wings have a pronounced violet iridescence.

[2] The ultraviolet reflection is strong at grazing incidence and arises only from the hingwings.

[3] The green colour is on the undersides of the hindwings; piliform scales.

[4] The green colour is on the undersides of the hindwings.

I. *Morpho*-type scales

In the subfamily Lycaeninae *Morpho*-type iridescent scales were present in the tribe Aphnaeini and in the subtribes Deudorigina and Hypolycaenina of the tribe Eumaeini, and are illustrated in Figs 1G, H, 2A, B, E–H, 3A, B, D–H, 4A, 6B, C. These scales are all of a type in which the flutes are tilted back towards the base of the scale and the scutes, when present, lie nearly parallel to the plane of the scale and directed towards the apex. In all species, it is found that each flute crosses the valley from one ridge to the adjacent one to form a continuous feature. On the sides of the ridges, the flutes become pronounced and closely periodic, to form multilayer surfaces, with each flute forming one element of the multilayer. This development gives rise to the iridescent coloration of these scales. Cross-sections of these scales show a typical "Christmas tree" form, due to the well-developed flutes. We term this microstructure *Morpho* (flute)-type.

Scutes appear to be absent or much reduced on *Spindasis syama* (Figs 1G, H), *S. nipalicus* (Figs 2A, B), *Artipe eryx* (Figs 3D–F), and *Hypolycaena erylus* (Figs 6B, C), and present on *Rapala rhoecus* (Figs 2E–G), *R. manea* (Figs 2H, 3A, B), and *Sithon nedymond* (Figs 3G,

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H, 4A).

In the *Spindasis* species (Aphnaeini) (Figs 1G–2B), and in *Rapala manea* (Deudorigina) (Figs 2H–3B), the flutes are, on average, out of vertical by less than about 40° so that the iridescent colour is only observed when the wing is tilted and will "flash on and off" in flight. In other species the flutes are more tilted so that the blue or violet colour is always visible; for example in *Rapala rhoecus* (Figs 2E, F) the flutes are at about 20° to the plane of the scale, in *Sithon nedymond* (Figs 3G–4A) at 30°, in *Hypolycaena erylus* (Figs 6B, C) at 30–45°. The iridescent scales in *Artipe eryx* (Figs 3D–F) take this trend to its limit. Over much (but not all) of the scale area the reflecting layers are parallel to the plane of the scale. This is most noticeable in the apical regions, and here the first 7 or 8 or so flutes run parallel to the ridge crests for considerable distances. Towards the base of the scales the flutes form reflecting surfaces at angles with the ridge crests and terminate below these crests.

II. *Urania*-type scales

The majority of the species examined were found to have scales of the *Urania* (pepper-pot)-type. These are not discussed individually here. What follows is a description of those scales that differ in some significant way from this norm.

Chliaria othona (Figs 6D–H) has a pale blue region on the forewings while the hindwings are almost completely pale blue. The blue scales are not strongly iridescent and only a small colour change is observed upon varying the angle of observation. These blue scales possess only one pepper-pot layer above the basal membrane, arrowed in Fig. 6G. No difference was found between the blue scales on the fore- or hindwings. Blue scales also have well developed flutes running perpendicular to the scale surface, shown in Fig. 6E. The structure of the ridges, with a "fir-tree" aspect, is illustrated in Fig. 6G. The apex of the forewing is dark and this region shows a pronounced purple iridescence when viewed at grazing incidence with the light from behind the observer. The apical scales do not possess a pepper-pot structure, but the flutes are developed into a *Morpho* (flute)-type structure, rather more pronounced than in the blue scales. Figs 6F, H show an apical scale revealing these features. In the central regions of the apical scales the flutes run virtually perpendicular to the scale surface, as on the blue scales. Cross sections of the apical scales confirm the lack of a pepper-pot interior and the presence of the "fir-tree" structure of a *Morpho*-type scale.

Siderus tephraeus has a rather similar upperside colour pattern to *Chliaria othona*, with largely blue hindwings and blue regions on the forewings together with dark apical regions. The blue of *tephraeus* is much deeper than that on *othona* and shows a considerable colour change as the viewing angle is altered. The iridescent blue scales are strongly curved (Fig. 4D), and the colour emanates from pepper-pot multilayers within the strongly curved scales, shown in Figs 4E, F. A pronounced purple iridescence is lacking in the dark brown apical region and here the scales are flat and strongly pigmented. However, despite the pigmentation, many of these scales are seen to have a reflected pale blue coloration in some orientations. They have a similar external morphology to the multilayer scales but contain only one pepper-pot layer, illustrated in Fig. 4G.

The scales of *Eumaeus minijas* are, as far as we know, unique to this genus. The obverse surface, with closely set microribs, shown in Figs 4H, 5A, is of the "satin" type (Ghiradella, 1984, 1985, 1998), but beneath the microribs *Urania*-type multilayers are present (Fig. 5B) though masked, so that iridescence is diminished.

The blue iridescent scales of *Anthene lycaenina* have an almost completely closed upper

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surface and superficially resemble the androconia found on the Polyommatina. The scales have a bag-like appearance and many present a curled appearance (Figs 11A–C). The few holes in the closed upper surface occur near to the apex of the scales. These permit one to establish the presence of a pepper-pot layer within the scale, as seen in Fig. 11D, and fractured scales reveal the multilayer nature of the internal structure.

Among the *Urania*-type scales are two in which the pepper-pot perforation is absent or very sparse, exemplified by the brassy green scales on *Arhopala aurea* (Figs 9C, D) and *A. eumolphus* (Figs 9E, F). In *Horaga syrinx* the internal structure resembles a lacework, seen in Fig. 7E, and in *Callophrys rubi* and *C. avis*, resembles crystallites as in Fig. 6A. *Poritia sumatrae* (Figs 1A, B) appears to show an early stage in the transition from a multilayer to crystallites.

III. Piliform and plume scales

Uniquely in the species reported here, the green iridescent colour on the underside hind wings of *Tomares ballus* arises not from flat scales but from piliform scales, illustrated in Figs 4B, C. Fractured cross-sections show a pepper-pot internal structure, which is responsible for the iridescent green appearance. The piliform scales in *T. ballus* are the only iridescent colour producers, and flat *Urania* (pepper-pot)-type scales are not present in this insect.

In a few of the species listed above, piliform scales of a similar colour to the major part of the wing surface are found and contribute to the appearance of the insect. To illustrate this, the basal area of the upper forewing of *Polyommatus coridon*, heavily clothed in piliform scales, is shown in Fig. 13E. This can be contrasted with Fig. 13F, which shows an area of wing devoid of piliform scales in which androconia (small scales), alternate with pale coloured blue scales and darker coloured backing scales. The piliform scales have a pepper-pot internal microstructure similar to that found on the flat scales in this species.

Piliform scales on the species utilising *Morpho* (flute)-type scales are generally of a brownish colour and do not show the stunning iridescence of the *Morpho*-type scales. Piliform scales intermixed with *Morpho*-type scales on the upper hindwings of *Spindasis syama* and *S. nipalicus*, thorax piliform scales adjacent to the upper side wings on *Rapala rhoecus* and *R. manea*, and piliform scales on the upper and lower wing surfaces of *Artipe eryx* were all examined. None showed any trace of a *Morpho*-like microstructure and fractured sections did not possess a *Urania* (pepper-pot)-type morphology.

Long, white, ribband-like scales, termed long plume scales by Eliot (1973), occur very widely throughout the tribe Polyommatini, but nowhere else in Lycaenidae, nor, as far as we know, in any other butterfly family. These scales vary in length according to species and differ from piliform scales in being flat, not circular, in section. Three examples are illustrated here. Fig. 11B shows a portion of the wing of *A. lycaenina* in which there is a scattering of long plume scales. The plume scales on *Polyommatus daphnis* (Fig. 13C) and *P. coridon* (Fig. 13F), differ from typical examples in that they are exceptionally short.

IV. Undifferentiated coloured scales

The coloured scales on a few species showed a lack of significant internal structure and none of these displayed a notable change of colour on tilting. In female specimens of *Rapala pheritima* (Fig. 3C) blue colours predominate and in three species, male specimens of *Curetis bulis stigmata* (Figs 1E, F), *Poecilmitis chrysaor* (Figs 2C, D), and *Lycaena virgaureae*

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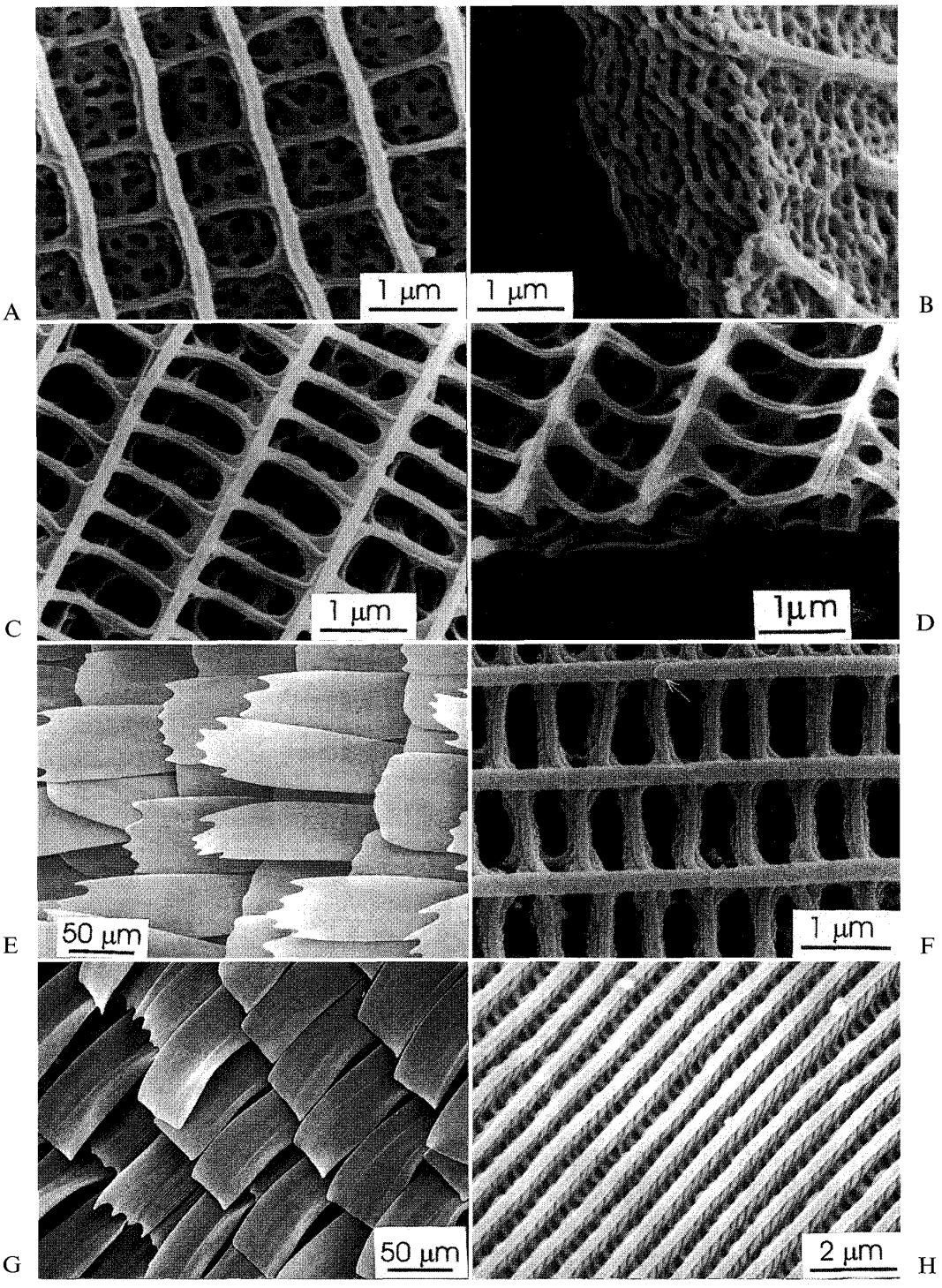

Fig. 1. A, B. *Poritia sumatrae*. A: pepper-pot scale; B: fractured scale showing complex interior layers. C, D. *Allotinus subviolaceus*. C: undifferentiated structure scale with wispy internal structure; D: fractured scale showing rudimentary perforated membrane. E, F. *Curetis bulis stigmata*. E: rounded and toothed scales are present; F: detail showing undifferentiated scale structure, with a scute arrowed. G, H. *Spindasis syama*. G: toothed backing scales with an undifferentiated structure and square-ended *Morpho*-type scales; H: an iridescent *Morpho*-type scale showing deep valleys between the ridges and well-developed flutes on the ridge sides.

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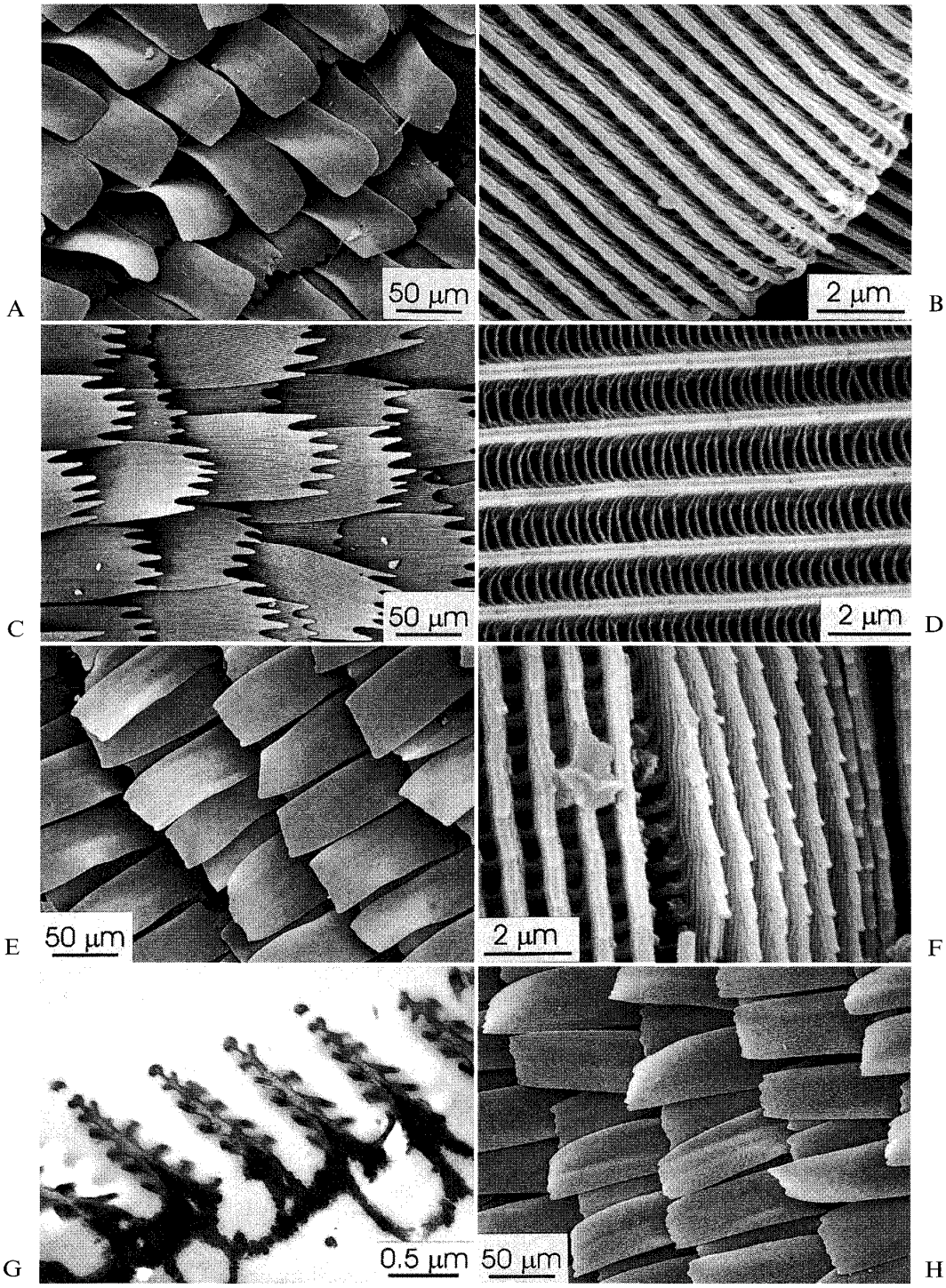

Fig. 2. A, B. *Spindasis nipalicus*. A: toothed backing scales with an undifferentiated structure and rounded *Morpho*-type scales; B: *Morpho*-type scale showing deep valleys between the ridges and well-developed flutes on the ridge sides. C, D. *Poecilmitis chrysaor*. C: toothed scales with an undifferentiated structure; D: scales showing closely spaced cross-ribs. E–G. *Rapala rhoecus*. E: square-ended *Morpho*-type scales; F: structure of a *Morpho*-type scale showing well-developed flutes that give rise to the iridescence; G: cross section of a *Morpho*-type scale showing the "fir-tree" arrangement of ridge flutes. H. *Rapala manea*, slightly toothed square-ended *Morpho*-type scale.

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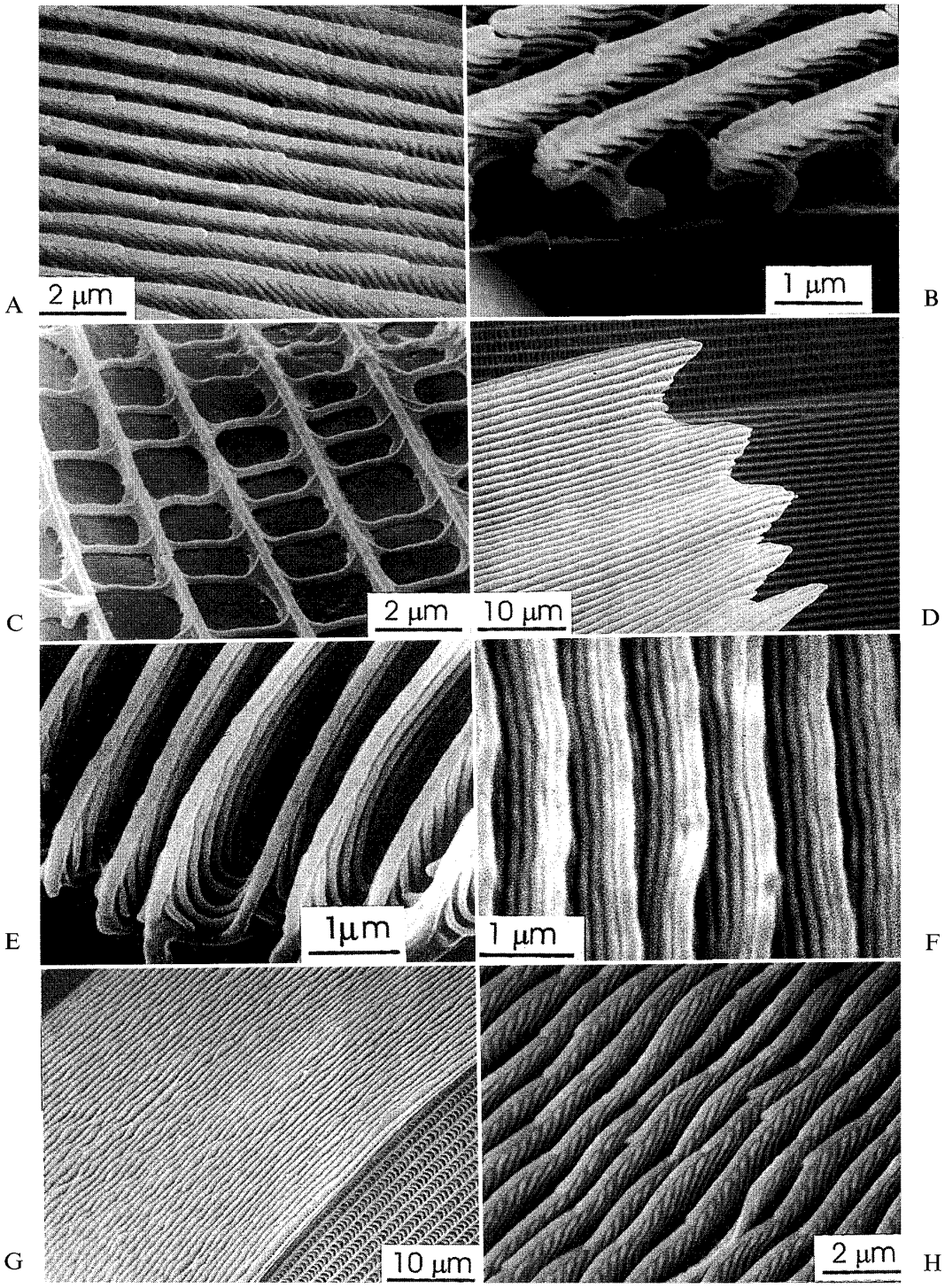

Fig. 3. A, B. *Rapala manea*. A: structure of an iridescent *Morpho*-type scale; B: fractured *Morpho*-type scale showing no internal layers, confirming that the flutes are the source of the iridescence. C. *Rapala pheritima*, female blue scales lacking a pepper-pot structure. D–F. *Artipe eryx*. D: toothed *Morpho*-type scale and backing scales with normal structure in the background; E: apex of *Morpho*-type scale showing the development of flutes into reflecting surfaces; F: structure of *Morpho*-type scales showing the flutes running parallel to the ridge crests. G, H. *Sithon nedymond*. G: a *Morpho*-type scale showing typical narrow ridge-spacing and deep inter-ridge valleys and a backing scale with undifferentiated structure in the background; H: structure of *Morpho*-type scales.

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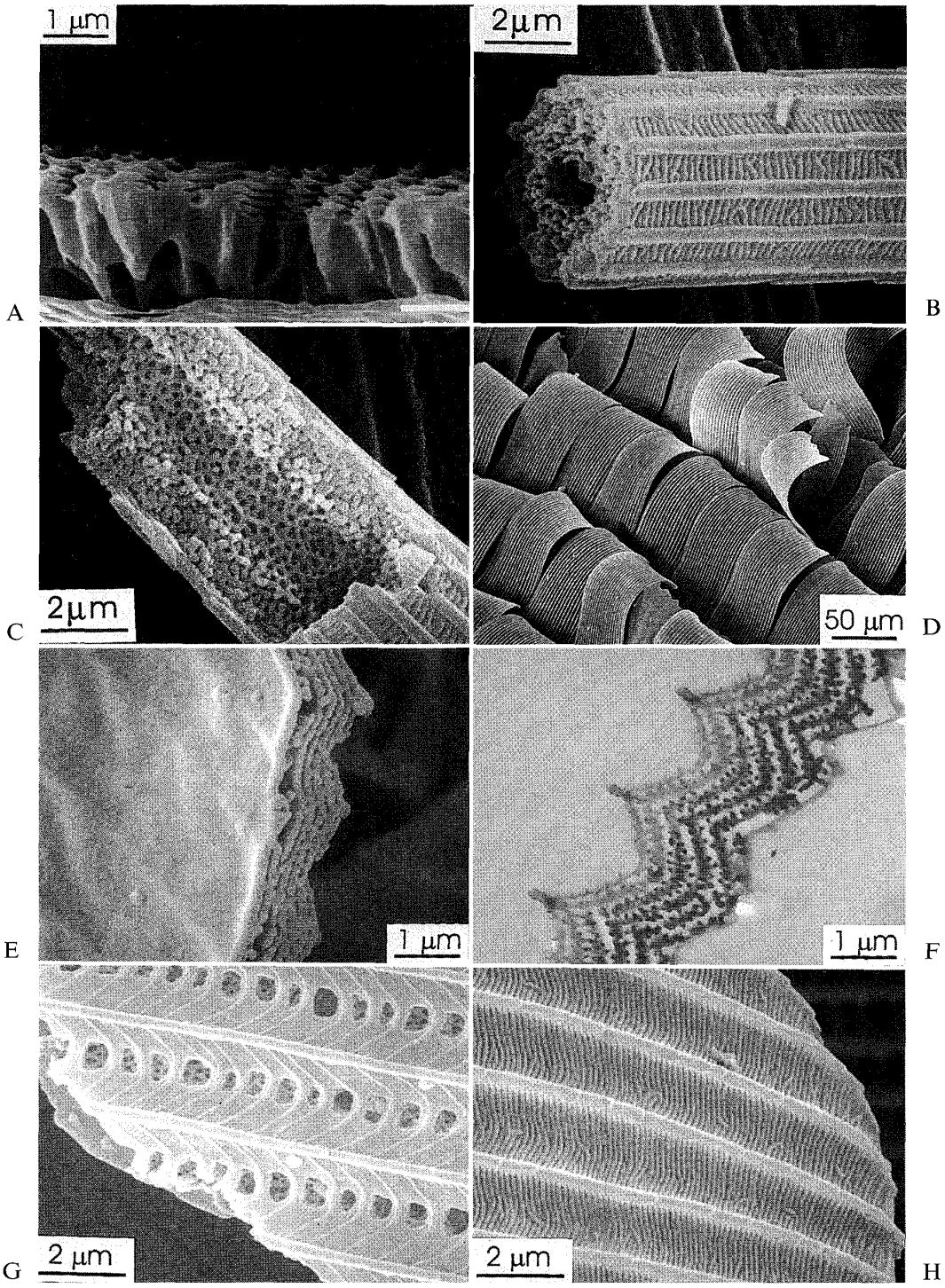

Fig. 4. A. *Sithon nedymond*, a fractured *Morpho*-type scale at grazing incidence, revealing the "fir-tree" arrangement of the ridge flutes. B, C. *Tomares ballus*. B: green piliform scale; C: fractured piliform scale revealing pepper-pot internal structure of the scale walls. D–G. *Siderus tephraeus*. D: curved iridescent scales; E: fractured iridescent scale from below, revealing the reverse surface and multilayer structure; F: cross section of an iridescent scale revealing the multilayer structure; G: scale from the dark brown apical region, showing an almost closed upper surface enclosing a single pepper-pot layer. H. *Eumaeus minijas*, apex area of iridescent scales.

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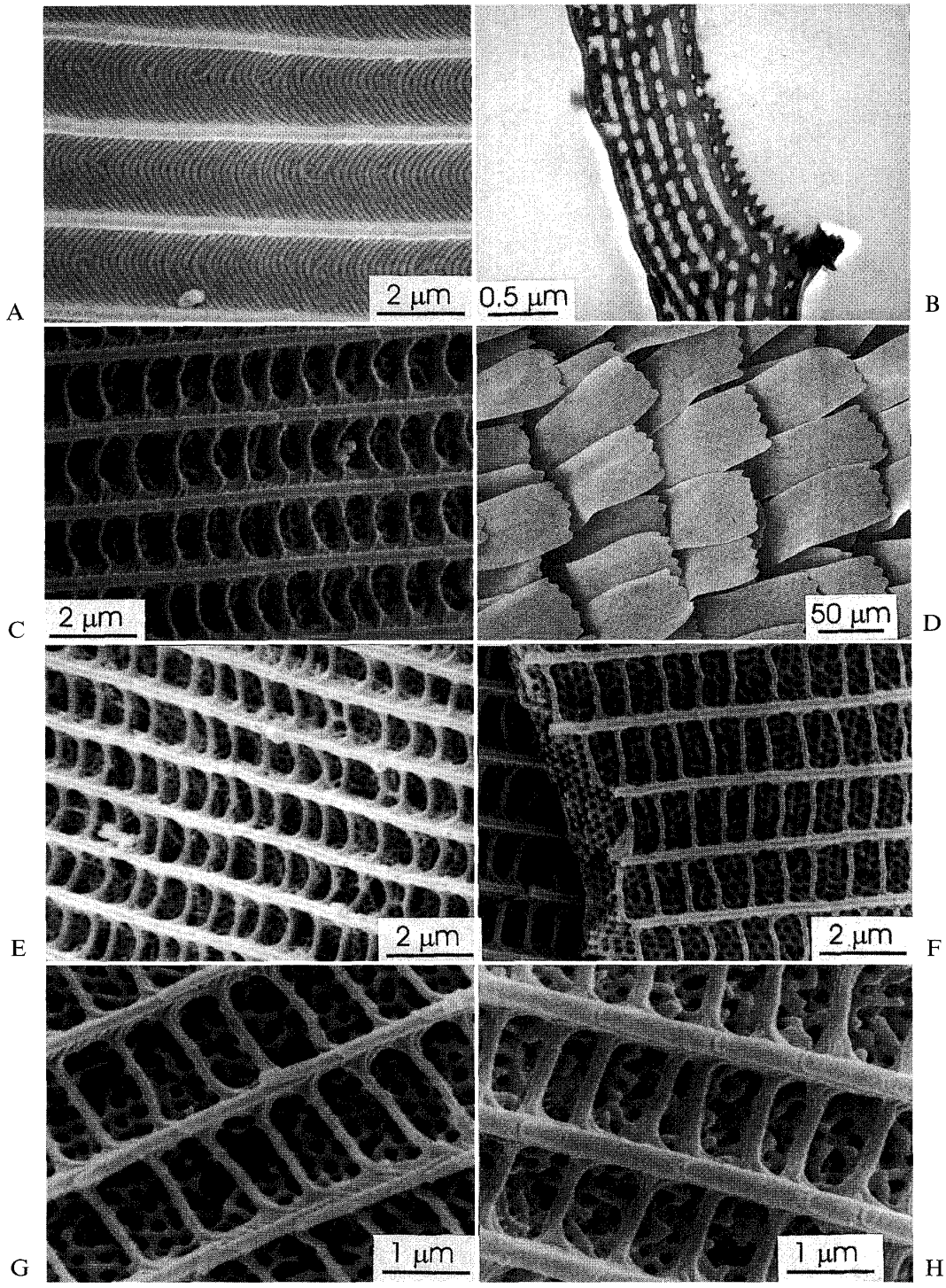

Fig. 5. A, B. *Eumaeus minijas*. A: closed upper surface of iridescent scales; B: cross section of an iridescent scale showing multilayer structure. C, *Atlides halesus*, pepper-pot structure of iridescent scales: D, E. *Arawacus meliboeus*. D: slightly toothed iridescent scales; E: pepper-pot structure of iridescent scales. F, G. *Callophrys rubi*. F: a fractured green scale showing multilayers; G: pepper-pot structure of green scales. H. *Callophrys avis*, pepper-pot structure of green scales.

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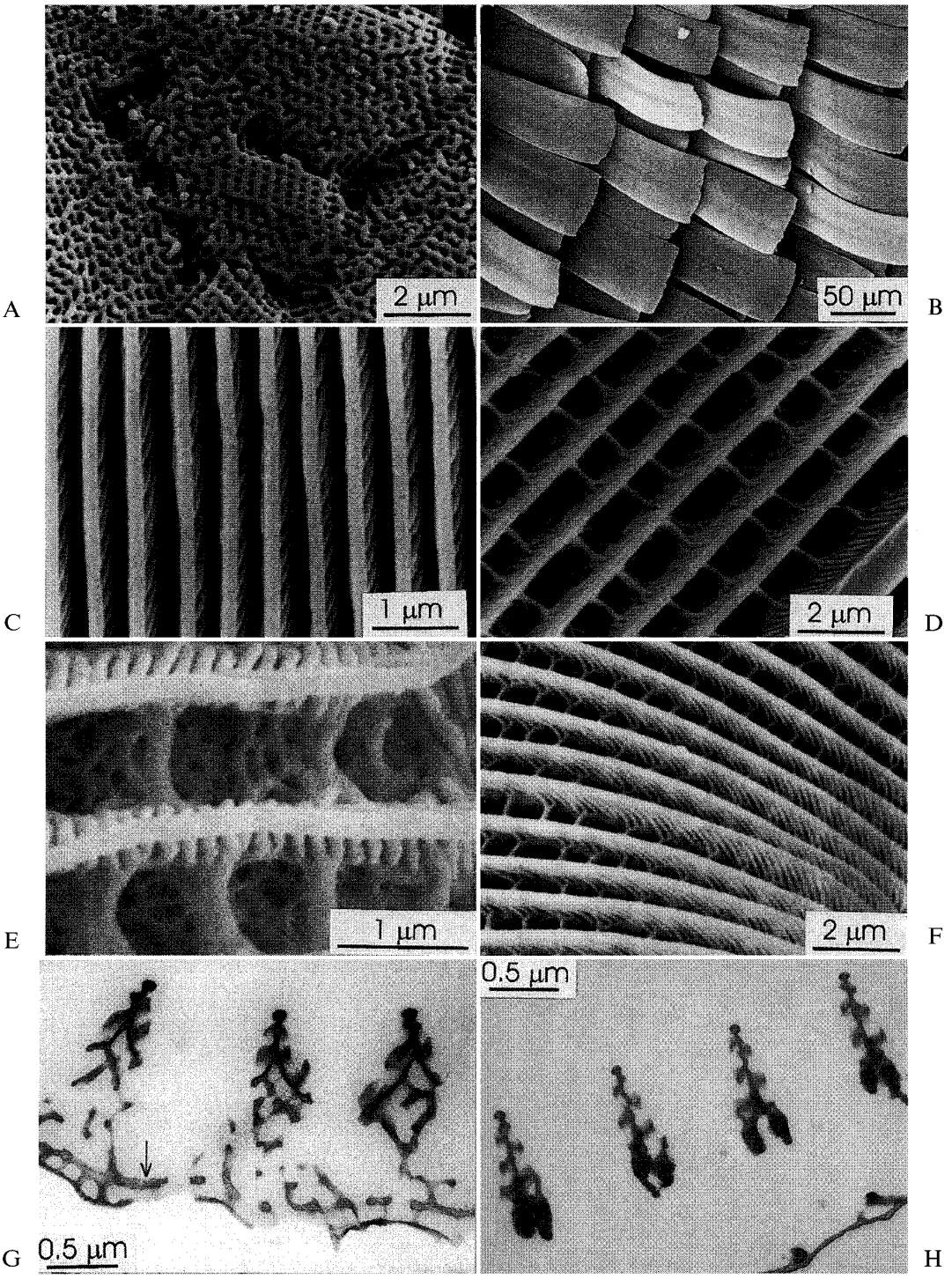

Fig. 6. A. *Callophrys avis*, "microdomain" structure of a scale interior, revealed by stripping the reverse surface from a scale. B, C. *Hypolycaena erylus*. B: square ended *Morpho*-type scales; C: structure of *Morpho*-type scales, showing deep valleys between the ridges and tilted flutes. D–H. *Chliaria othona*. D: pepper-pot structure of a blue scale; E: pepper-pot blue scale showing prominent flutes; F: towards the apex of a brown apical scale, revealing no internal pepper-pot structure but well developed flutes; G: cross-section of a blue scale showing a single pepper-pot layer, arrowed, above the reverse surface and the discernable "fir-tree" structure of the ridges. H. cross section of a brown apical scale revealing the "fir-tree" structure of the ridges and a single reverse surface.

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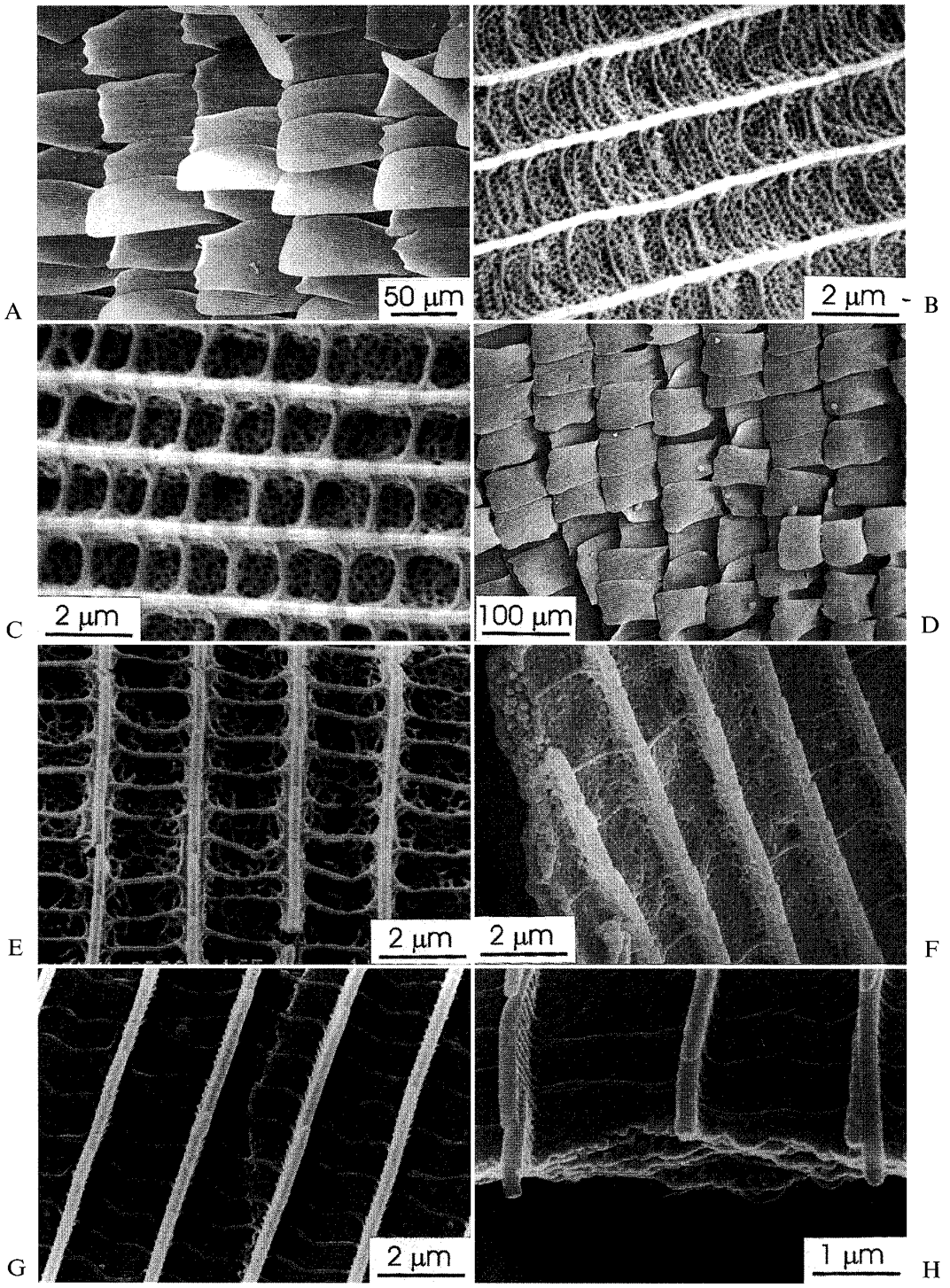

Fig. 7. A, B. *Catapaecilma major*. A: rounded violet-blue scales with some toothed backing scales also visible; B: pepper-pot structure of violet-blue scales. C. *Drina maneia*, pepper-pot structure of deep-blue scales. D, E. *Horaga syrinx*. D: rather square blue scales; E: pepper-pot structure of blue scales. F. *Drupadia ravindra*, fractured blue scale showing pepper-pot structure and multilayers. G, H. *Iraota rochana*. G: turquoise pepper-pot scale; H: fractured pepper-pot scale showing multilayers.

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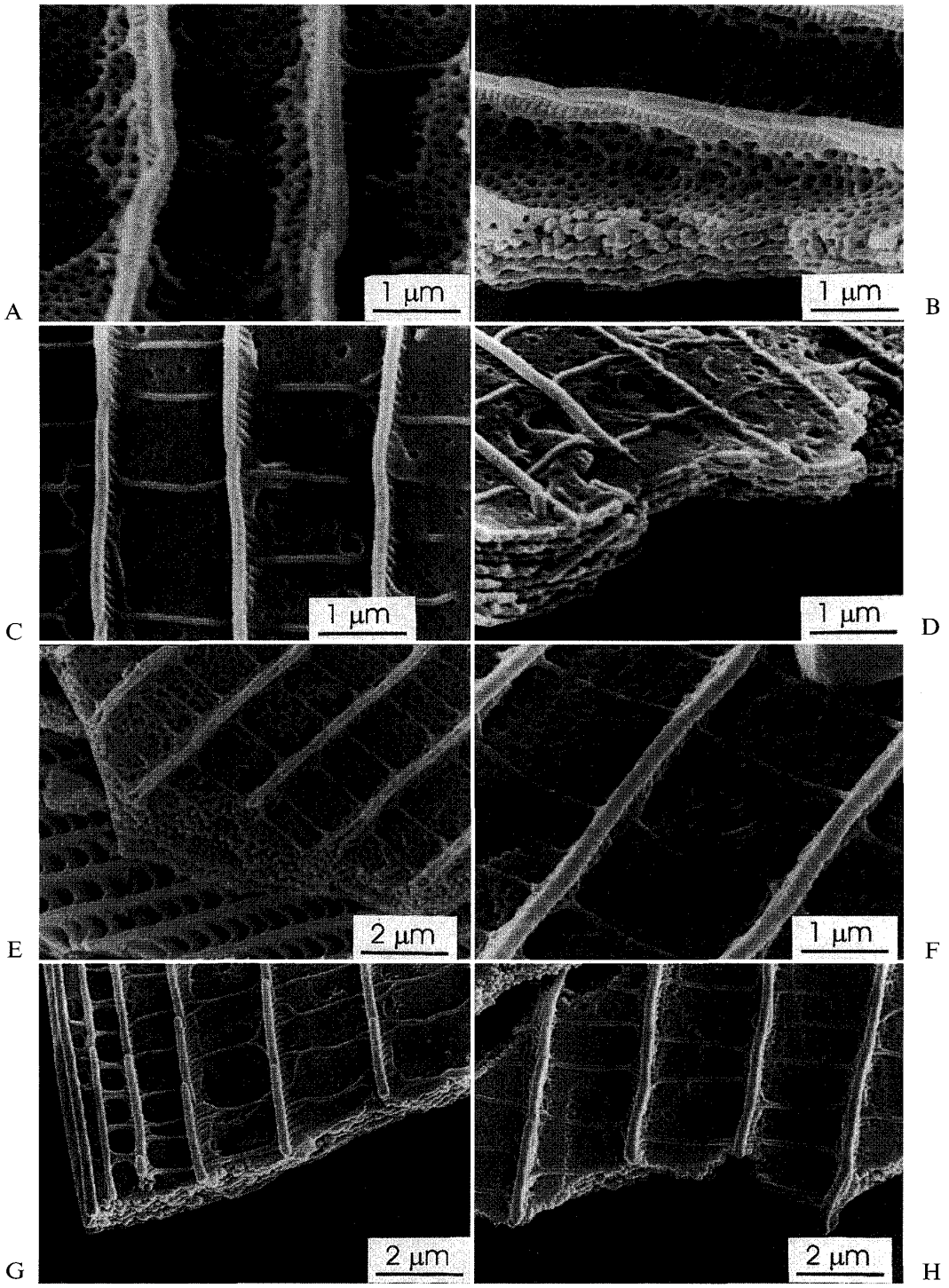

Fig. 8. A, B. *Tajuria cippus*. A: blue pepper-pot scale; B: fractured scale showing multilayers. C, D. *Remelana jangala*. C: violet-blue scale with a minimal pepper-pot structure; D: fractured pepper-pot scale showing the multilayer structure. E. *Ancema blanka*, fractured pepper-pot scale showing the multilayer structure, overlaying a normal backing scale. F, G. *Quercusia quercus*. F: purple scale with a minimal pepper-pot structure; G: fractured pepper-pot scale showing the multilayer structure; H. *Laeosopis evippus*, purple scale with a minimal pepper-pot structure.

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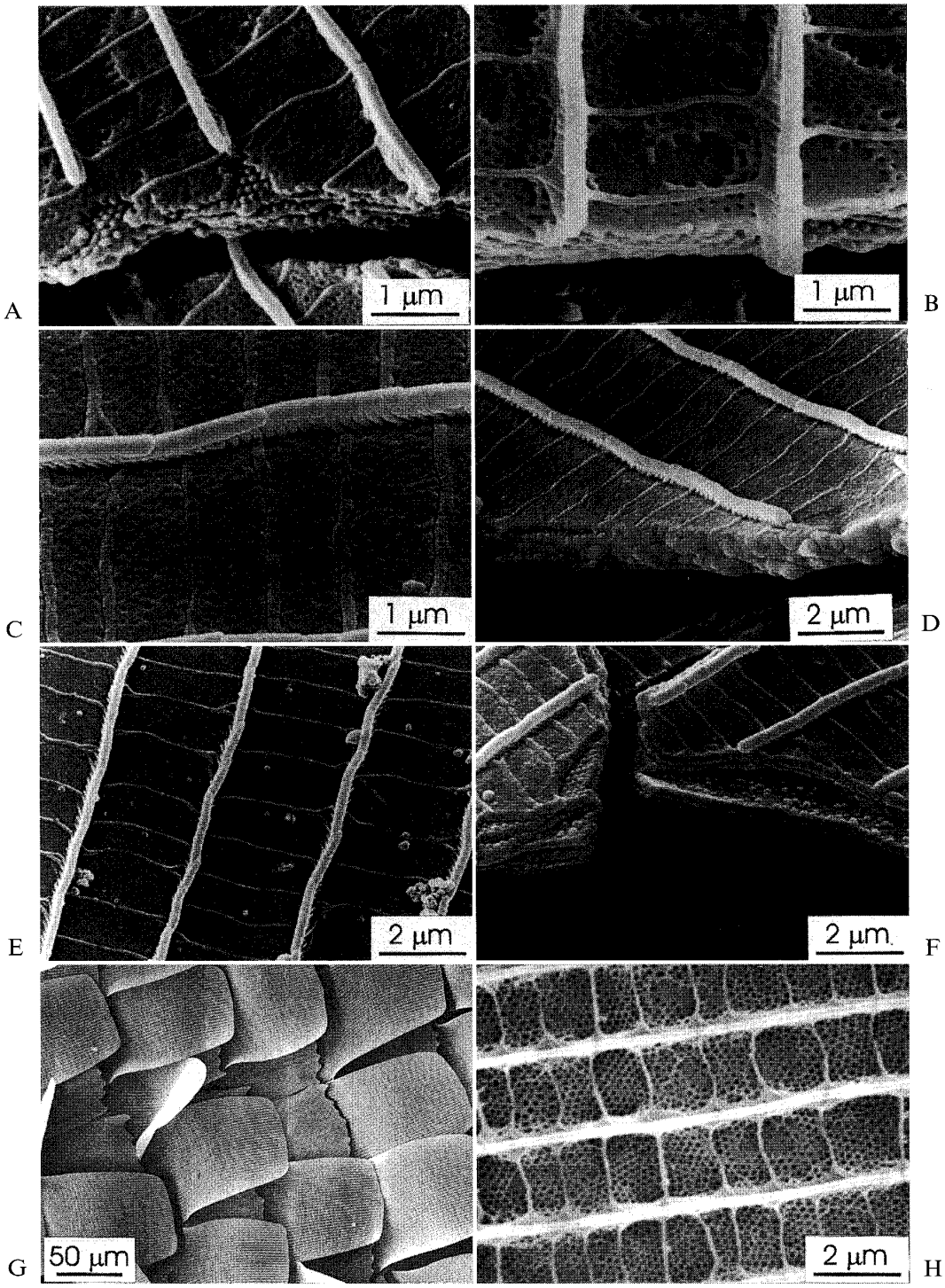

Fig. 9. A. *Laeosopis evippus*, fractured scale showing the multilayer structure. B. *Arhopala pseudocentaurus*, fractured pepper-pot scale showing the multilayer structure. C, D. *Arhopala aurea*. C: gold-green scale with a minimal pepper-pot structure; D: fractured scale showing the multilayer structure. E, F. *Arhopala eumolphus*. E: green-gold scale with a minimal pepper-pot structure; F: fractured scale showing the multilayer structure. G, H. *Surendra florimel*. G: rounded deep-blue scales with some slightly toothed backing scales also visible; H: pepper-pot structure of blue scales.

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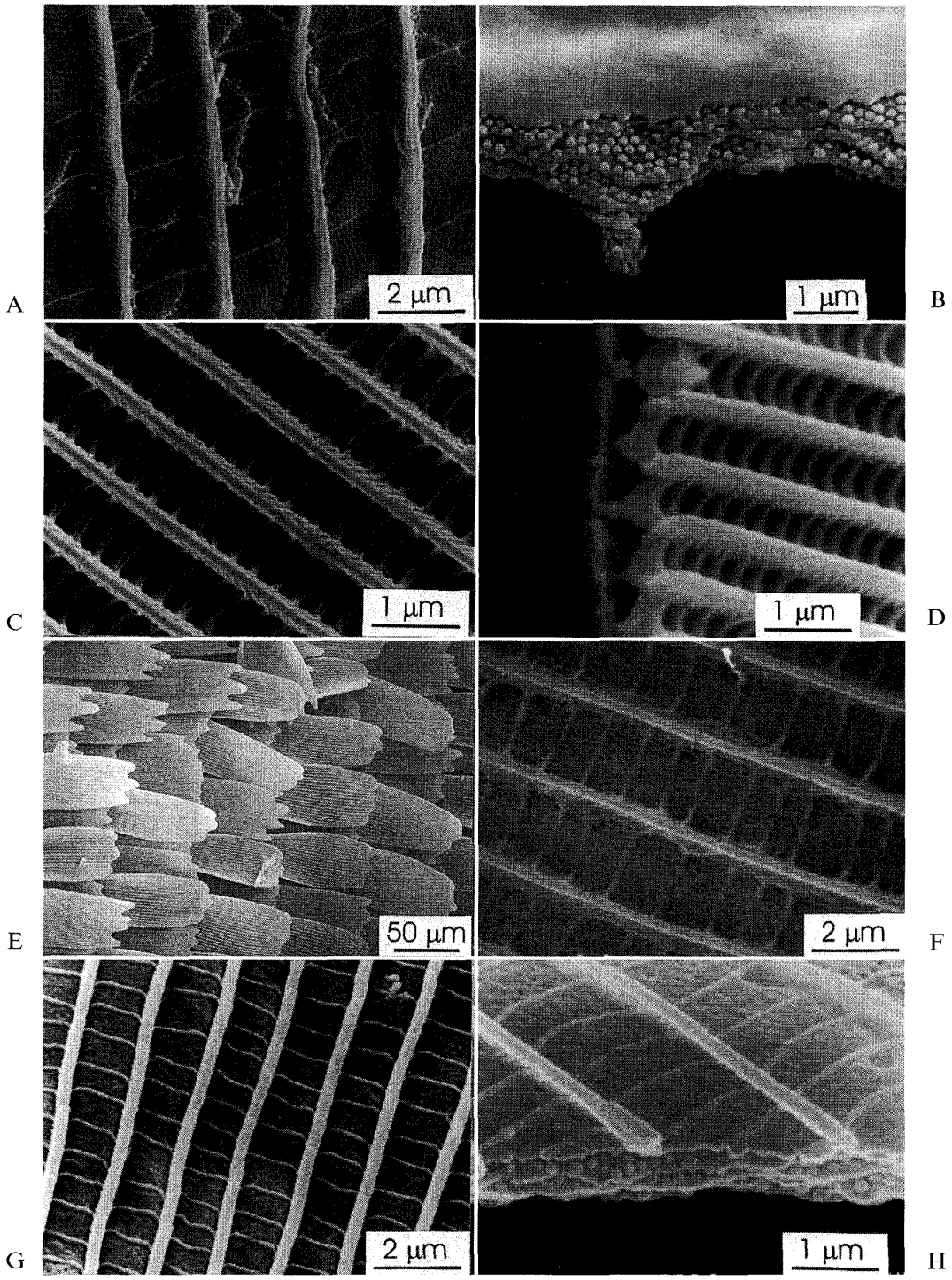

Fig. 10. A, B. *Surendra vivarna*. A: pepper-pot structure of deep blue scales; B: view of a fractured pepper-pot scale from below showing the reverse surface and multilayer structure. C, D. *Lycaena virgaureae*. C: undifferentiated structure of shining orange scales; D: a fractured orange scale showing no internal structure above the reverse surface. E, F. *Lycaena alciphron*. E: slightly toothed scales giving rise to the purple-shot effect and toothed copper-coloured scales; F: pepper-pot structure of purple-shot scales. G, H. *Heliophorus androcles*. G: sky-blue scale with a minimal pepper-pot structure; H: fractured scale showing the multilayer structure.

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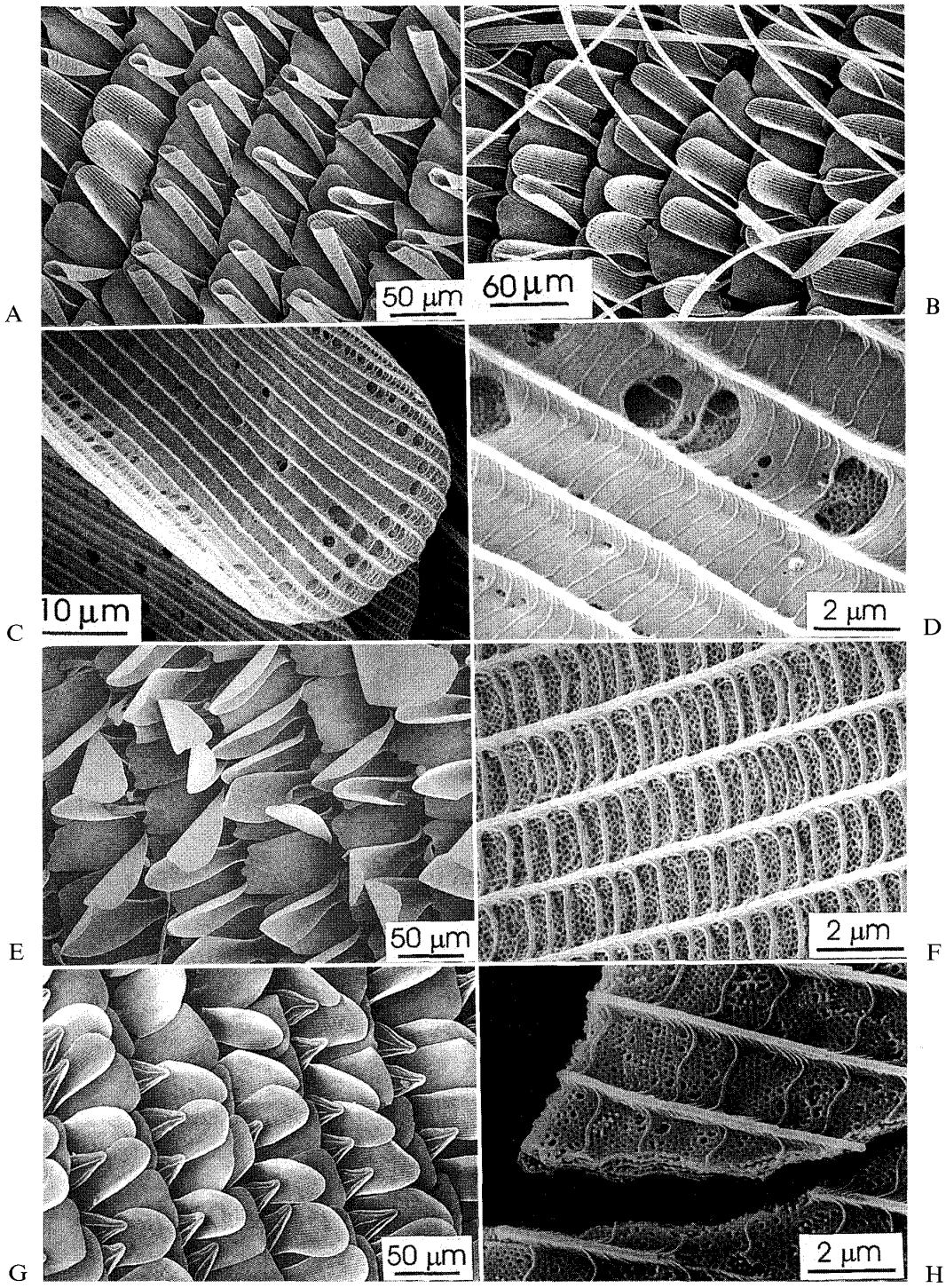

Fig. 11. A–D. *Anthene lycaenina*. A: violet-blue iridescent scales, mostly strongly curved, and squarer backing scales; B: another area of forewing, showing scattered long plume scales in addition to rounded iridescent scales and squarer backing scales; C: violet-blue scale showing bag-like appearance with few perforations in the obverse surface; D: pepper-pot structure of the violet-blue scales visible below the obverse surface. E, F. *Candalides margarita*. E: indigo scales, mostly strongly curved, and slightly toothed backing scales; F: pepper-pot structure of indigo scales. G, H. *Niphanda tesselata*. G: rounded deep-blue scales, square backing scales and numerous smaller androconia; H: fractured deep-blue scale showing pepper-pot structure and multilayers.

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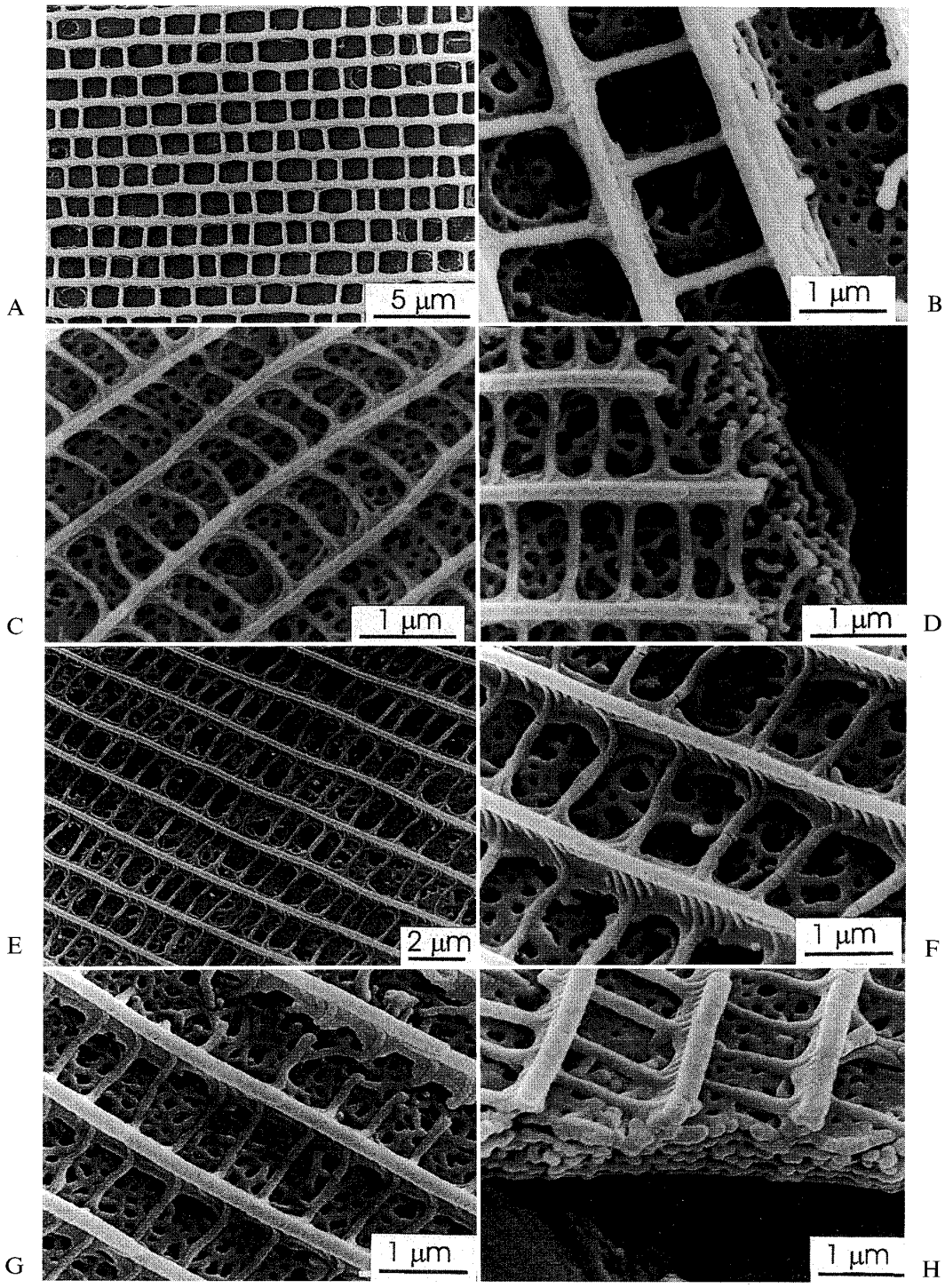

Fig. 12. A, B. *Jamides caeruleus*. A: sky-blue scales showing square "windows" on obverse surface; B: pepper-pot structure of sky-blue scales. C, D. *Celastrina argiolus*. C: sky-blue scale showing pepper-pot structure; D: a fractured scale showing the multilayer structure. E, F. *Cupido minimus*. E: blue scale from a male butterfly; F: blue scale showing pepper-pot structure. G, H. *Glaucopsyche alexis*. G: blue scale showing pepper-pot stucture; H: fractured scale showing the multilayer structure.

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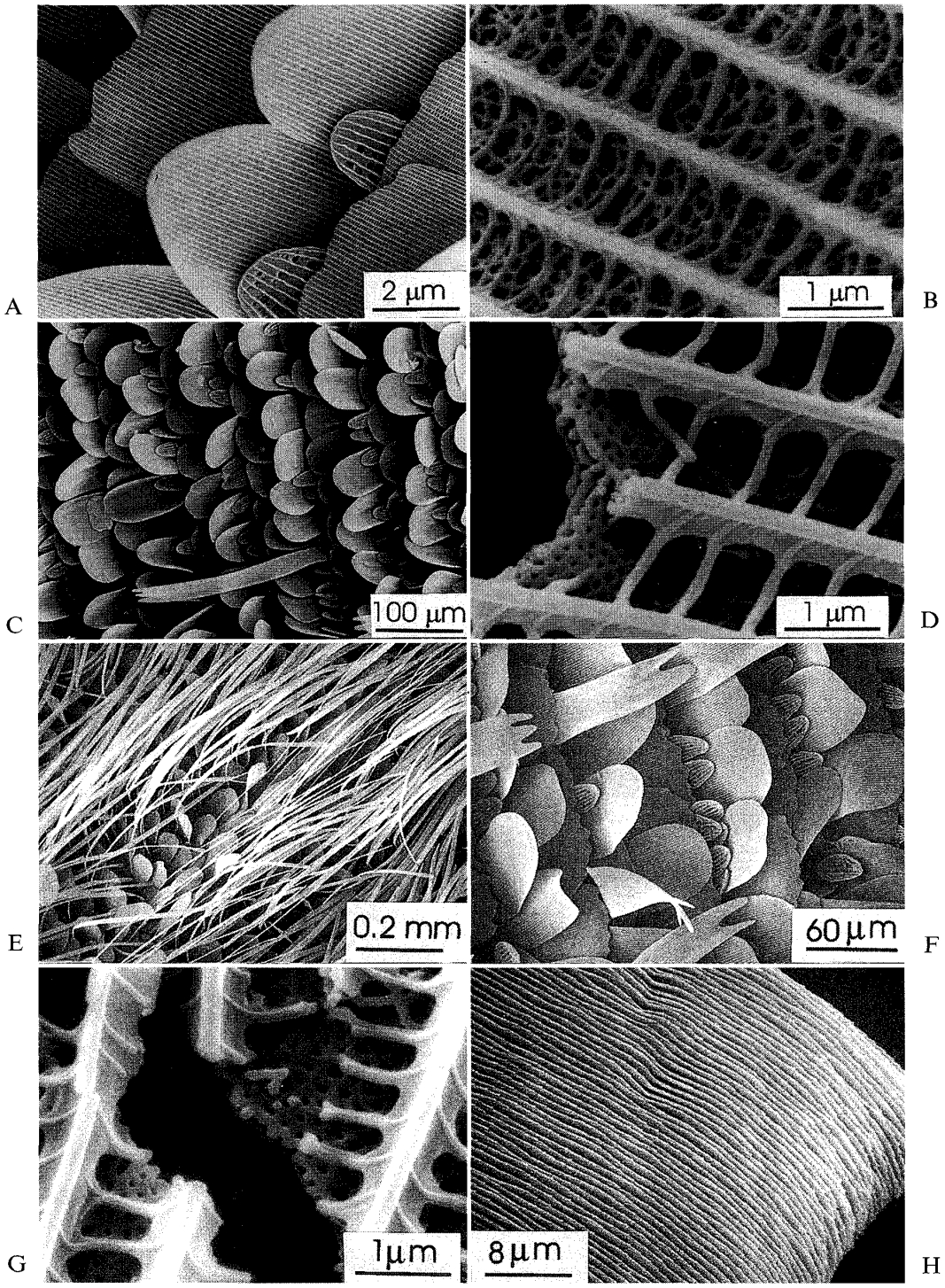

Fig. 13. A, B. *Polyommatus escheri*. A: rounded blue scales, toothed darker backing scales and small androconia; B: blue scale showing pepper-pot structure. C, D. *Polyommatus daphnis*. C: blue scales (light), backing scales (dark) and small androconia; D: fractured blue scale showing pepper-pot multilayer structure. E–G. *Polyommatus coridon*. E: basal area of upper forewing showing dense piliform scales, some of which are flattened rather than round; F: upper forewing area devoid of piliform scales showing androconia (small), rounded blue scales (mostly light), slightly toothed backing scales (mostly dark) and short plume scales; G: fractured blue scale showing internal pepper-pot microstructure. H. *Lyropteryx lyra*, curved iridescent scale.

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(Figs 10C, D), the colours are a shining copper-orange. These scales possess an undifferentiated scale structure and resemble pigmented scales elsewhere on the wings. The origin of the colour of all these scales merits further investigation.

In the "copper" *Lycaena alciphron*, the copper coloured scales have an undifferentiated structure (not illustrated), and the scales giving a violet suffusion, shown in Figs 10E, F, have a pepper-pot structure. It is only these latter scales that are mentioned in Table 1.

Female specimens of *Allotinus subviolaceus* (Figs 1C, D) are also recorded as having an undifferentiated scale structure in Table 1. In general, a few wispy features are visible within the scales of this species, and in some regions these form a quite well defined membrane perforated by large irregular holes, as seen in Fig. 1D.

V. Riodinidae

The seven species of Riodinidae examined are listed in Table 2. The Old World species, *Hamearis lucina*, *Abisara echerius*, and *Paralaxita telesia* do not show iridescence. In this study, the upper-side of the wings of these three species were examined. All have undifferentiated pigmented scales that are not illustrated. The diffuse purple colour of *A. echerius* has not been investigated in detail, but it does not arise from either *Morpho*-type or *Urania*-type structures. The four New World genera examined, all of which show iridescence, were *Lyropteryx lyra* (Figs 13H, 14A, B), *Ancyluris meliboeus* (Figs 14C, D), *Rhetus periander* (Fig. 14E), and *Lasaia narses* (Fig. 14F). *Ancyluris meliboeus* is unusual in that the blue iridescent scales are on the undersides of the wings. It was found that the iridescent scales on three species, *Lyropteryx lyra*, *Ancyluris meliboeus* and *Rhetus periander*, have a "classical" *Morpho*-type reflecting structure formed by the development of the ridge scutes. This morphology, which we term *Morpho* (scute)-type, is clearly visible in Figs 14A–E. The shining electric blue of *L. narses* has a different origin, and neither *Urania*- nor *Morpho*-type scales are present. The iridescent scale structure on this species (Fig. 14F) appears to be similar to the shining orange scales of male "copper" butterflies, as can be judged by a comparison of Fig. 14F with Fig. 10C (*Lycaena virgaureae*).

No traces of *Urania*-type microstructures were observed in the seven specimens examined.

Discussion

Previously it was thought that the structural scales on the upper surface of the wings of all Lycaenidae were, broadly speaking, of the *Urania*-type (Eliot, 1973). The discovery of *Morpho* (flute)-type scales in two subtribes, Deudorigina and Hypolycaenina, of the tribe

Table 2. Species of Riodinidae examined.

species	sex	colour	scale type*	ridge type*
Old World species				
Hamearis lucina (Linnaeus, 1758)	♂	orange	undiff	moderate, ~1.3 μm
Abisara echerius (Stoll, 1790)	♂	brown	undiff	moderate, ~1.35 μm
Paralaxita telesia (Hewitson, 1861)	♂	brown/rust	undiff	moderate, ~1.3 μm
New World species				
Lyropteryx lyra Saunders, 1859	♂	green	*Morpho*-type	deep, ~0.6 μm
Ancyluris meliboeus (Fabricius, 1793)	♂	blue	*Morpho*-type	deep, ~0.9 μm
Rhetus periander (Cramer, 1777)	♂	blue	*Morpho*-type	deep, ~0.45 μm
Lasaia narses Staudinger, 1888	♂	blue	undiff	moderate, ~1.5 μm

* The same terminology is used as in Table 1.

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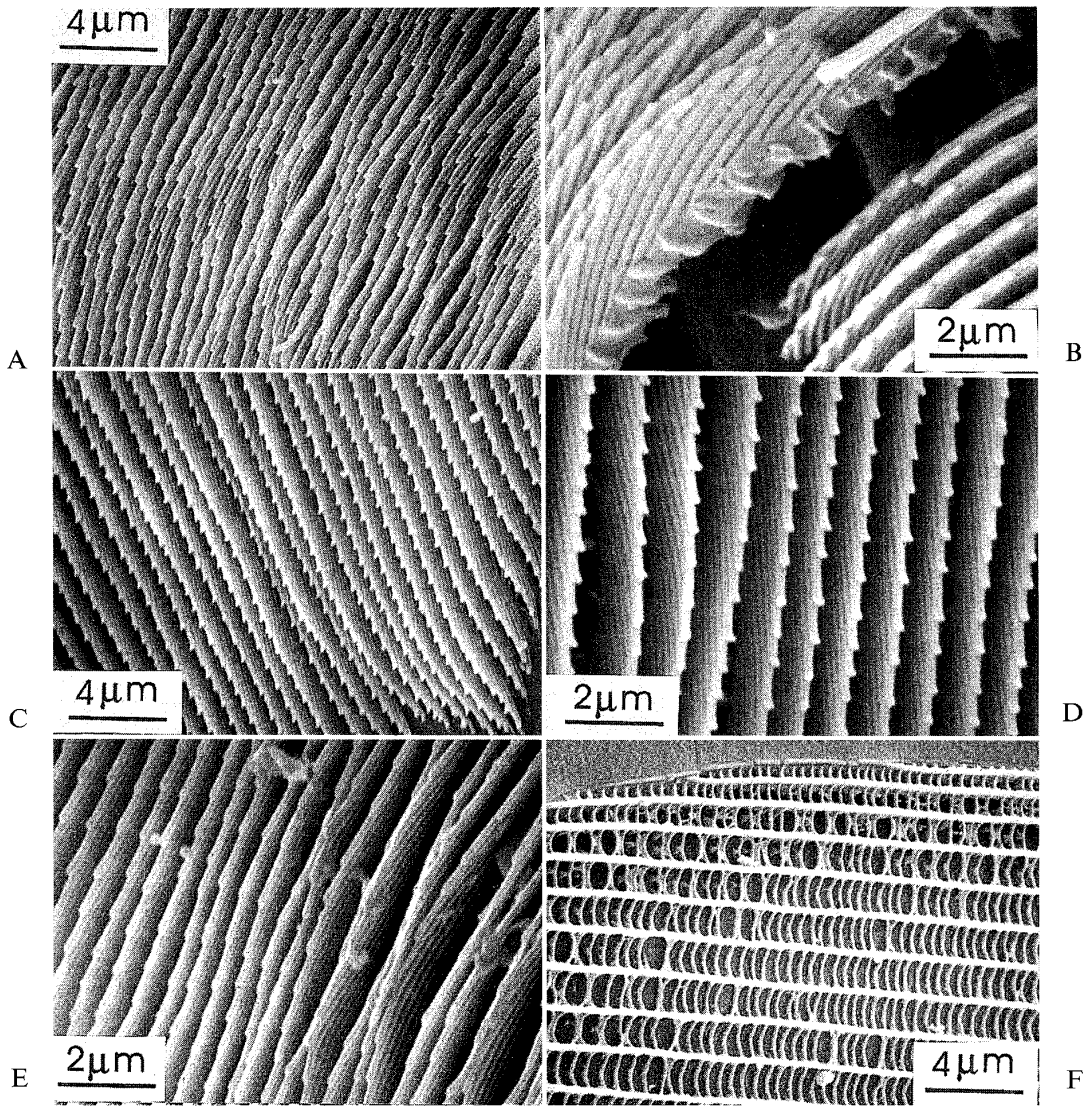

Fig. 14. A, B. *Lyropteryx lyra*. A: iridescent scale showing very deep valleys between ridges; B: fractured scale revealing the *Morpho* (scute)-type microstructure. C, D. *Ancyluris meleboeus*. C: apex of iridescent scale revealing deep valleys between ridges; D: *Morpho* (scute)-type microstructure on the ridge sides. E. *Rhetus periander*, *Morpho* (scute)-type microstructure of iridescent scales. F. *Lasaia narses*, normal scale structure with no *Morpho*- or *Urania*-type microstructures.

Eumaeini and in the tribe Aphnaeini adds a new dimension to the data.

In considering the significance of these results, we first discuss structural aspects, especially those scales that differ in some significant respect from the common *Urania* (pepper-pot)-type. Then we consider whether scales can provide useful characters in determining phylogeny and taxonomy. Finally, we consider whether, in Lycaenidae, *Urania*-type scales have transmuted into *Morpho* (flute)-type scales.

I. Scale structures

In the species possessing *Morpho*-type scale morphology examined here, only the flutes have developed to produce structures capable of giving rise to iridescence, and this is emphasised by the terminology *Morpho* (flute)-type. In the species *Chliaria othona*, which, uniquely to

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date, possesses both *Morpho*- and *Urania*-type colour-producing elements on the same scale, the *Morpho*-type features also arise from well-developed flutes. Although this morphology does not play as significant a role in *Chliaria othona* as in the other species with *Morpho* (flute)-type microstructures, the purple iridescence visible at grazing incidence in the apical scales is explained by the presence of this feature. Moreover, the angle of the flutes to the surface accounts for the precise lighting conditions needed for observation of the iridescence.

The *Morpho* (flute)-type microstructures are quite different from the *Morpho* (scute)-type of scales found in the Riodinidae (Figs 13H–14E), Nymphalidae (Downey & Allyn, 1975; Ghiradella, 1984, 1985, 1994; Sellier, 1971), Pieridae (Ghiradella, 1984, 1991; Sellier, 1971), and Papilionidae (Meyer-Rochow & Eguchi, 1983; Ghiradella, 1985), where the development of the scutes is clear. In this respect, the absence of scutes in some species showing *Morpho*-type microstructures does not seem to be significant. Scales showing weak or no scute development have been reported previously across several families (Downey & Allyn, 1975; Ghiradella, 1998). Additionally, the *Morpho* (flute)-type microstructures found here do not resemble those on species in which the whole of the ridge structure is "rocked back" towards the base of the scale, thus allowing flutes to create a reflective surface (Ghiradella, 1998, fig. 22D). The *Morpho* (flute)-type microstructures reported here thus seem, with one possible exception detailed below, to be characteristic of lycaenid butterflies.

The intensity of the iridescence from a *Urania*-type scale increases with the number of internal layers present, and strongly iridescent scales seem to have four or more lamellae present, as shown in Figs 4F, 5B, 8A, D and elsewhere. It is therefore possible that the pale blue weakly iridescent coloration seen on *Chliaria othona* is due to the presence of a single pepper-pot layer in the blue scales. This feature is not found in the apical scales, and here no blue coloration is observed. A further species, *Siderus tephraeus*, is also of relevance here. In this species, multilayer pepper-pot scales coexist with single pepper-pot layer scales. The single pepper-pot layer is found in the pigmented apical scales and only these scales exhibit a weak blue cast. This is in contrast to the strong colour produced by the iridescent scales that have five or more layers present.

Allotinus subviolaceus has a similar pale blue colour to both of the last species, but a well-formed single pepper-pot layer could not be discerned. Instead, a filmy membrane is found. This feature does not appear to form a coherent intermediate layer, but may represent an incipient single pepper-pot layer, to some extent recalling the single layer in *Chliaria othona* and *Siderus tephraeus*. It is possible that this layer is sufficiently developed to be the source of the blue colour on this butterfly.

Piliform scales and flat scales, are homologous structures (Ghiradella, 1998). Piliform scales take on a great significance in *Tomares ballus* as they are the only iridescent colour producers. Although these have an internal pepper-pot microstructure, flat *Urania* (pepper-pot)-type scales seem not to have evolved in this insect, as they have, for example, in *Polyommatus coridon*, which also has piliform scales with an internal pepper-pot structure. From this point of view, it is of interest to note that the piliform scales occurring on the species possessing *Morpho* (flute)-like scales studied here did not show a *Morpho* (flute)-like morphology.

II. Phylogenetic and taxonomic implications

In discussing phylogenetic and taxonomic implications of this study, a caution must be emphasised. We have only examined about 1% of the species of Lycaenidae, and if those

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examined by other authors are added the total is still probably well below 2%. The same can be said of other families, except perhaps, Papilionidae. Any inferences drawn from a study of scales must, therefore, be treated as provisional.

So far scales have not been used in phylogenetic or taxonomic studies because of the occurrence of similar types in more than one family (Ghiradella, 1985). Although this fact is certainly a severe handicap, we think that scales have a limited role to play, especially at the infra-family level. Even at the supra-family level, scales may occasionally serve a taxonomic purpose. The fact that the *Urania* (pepper-pot)-type structure of the most common iridescent scales in Lycaenidae has not been reported from any other butterfly family makes it a significant phylogenetic character. It may also be significant that apart from the species described in this paper, a *Morpho* (flute)-type scale has only been found in one extraneous species, the Birdwing *Trogonoptera brookiana*. In this insect, iridescent green scales on the upperside and blue scales that occur in a small area on the wing undersides have a reflecting structure built from developed flutes and resemble the iridescent scales of *Artipe eryx* (Ghiradella, 1985)[1)].

The Riodinidae illustrate this aspect further. There are conflicting opinions as to whether this group should be treated as a subfamily, sister to the remaining Lycaenidae (Scott & Wright, 1990; de Jong *et al.*, 1996; Ackery *et al.*, 1998), as a distinct family sister to the Lycaenidae (Harvey, 1987; De Vries, 1997; Campbell *et al.*, 2000) or as a distinct family sister to the Nymphalidae (Robbins, 1988; Martin & Pashley, 1992). The fact that none of the various types of lycaenid structural scales have been found in Riodinidae whilst the only structural scales found in Riodinidae are the same and sole type recorded from the Nymphalidae provides a fresh argument in favour of the view that Riodinidae and Nymphalidae are sister groups.

At the infra-family level of Lycaenidae the first need is to decide which type of scale came first. To solve this problem it is necessary to consider the lycaenid population of South America. Here the family is represented only by the subtribe Eumaeina, apart from some Andean Polyommatina which have entered from North America after the junction of the two continents in the Pliocene, and a very few others whose presence is easily explicable by waif or recent dispersal. For reasons that it would be inappropriate to enter into here, we believe that the origin of the Lycaenidae lies in the Eurasian part of Laurasia in the early Cretaceous. Entry of Lycaenidae into the Africa/South America remnant of Gondwana would have been by the "Gibraltar route" and it is logical to believe that at the time of parting of the two continents, around the mid-Cretaceous, only ancestral Eumaeini were present; otherwise other units of the Lycaenidae would be present in South America today. As only *Urania*-type scales have been found in Eumaeina, it is reasonable to suppose that they were the original structural scales in Lycaenidae, and that the *Morpho*-type evolved in Africa, either independently or by transmutation, after the parting of the continents. A further reason for supposing that *Urania*-type scales came first lies in their occurrence in Poritiinae. It is generally held that the primary division of the lycaenid stem led to the separation of Lycaninae from a branch leading to Poritiinae, Miletinae and Curetinae. Thus, it can be assumed that *Urania*-type scales were already present at this very early stage.

Turning to the three taxa that now have *Morpho* (flute)-type scales we deal first with Deudorigina and Hypolycaenina. These two subtribes have been considered to be closely

[1)] It is of interest that in another green Birdwing, *Ornithoptera priamus*, the scales are of a modified *Urania*-type (Ghiradella, 1985).

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related to one another and to the Eumaeina because of their shared adult morphological characters of "greyhound-shaped" genitalia, lacking a juxta and with conjoined or adjacent valvae, as well as the loss of at least one forewing vein. Both the former subtribes have their headquarters in Africa, whence they have spread to the Oriental Region and the southeastern fringes of the Palaearctic, probably only after India collided with Asia and provided a route for their dispersal. This scenario is compatible with the proposal that their *Morpho* (flute)-type scales evolved in Africa after it was isolated from the other continents.

The Aphnaeini, with only a few species possessing iridescent scales, present a more difficult case. Hitherto they have been thought to be the earliest offshoot of the subfamily Lycaeninae (Eliot, 1973; Scott & Wright, 1990; Fiedler, 1991). There are two reasons for this. Firstly the early stages, in which the larval head is not retracted and in which their specialised myrmecophilous organs are present from the first instar, are distinctive. Secondly, alone in the subfamily, the adults sometimes retain all twelve forewing veins in both sexes as well as all components of the male genitalia. In the remainder of the subfamily the larval head is fully retractable, myrmecophilous organs, if present, are simpler and present only from the second or later instar, and one, often two, veins are lost from the forewing except in males of a handful of species. If, indeed, Aphnaeini were the earliest offshoot, one would expect them to have a wide distribution. In fact, their distribution is even more restricted than that of Deudorigina and Hypolycaenina, with only a few species reaching the southern fringes of the Palaearctic and more reaching the Oriental Region, presumably having dispersed there via India, after its collision with Asia. Thus, there is a case for supposing it might be the last, rather than the first, tribe to evolve. The distinctive early stages are not a bar to this possibility, since it seems that virtually all Aphnaeini larvae are obligate myrmecophiles, and this could account for their non-retractable head and highly specialised ant organs. The only difficulty lies in their adult venational and genitalic characters, which make it inconceivable that they evolved from the branch that gave rise to the Eumaeina, Deudorigina and Hypolycaenina. Thus, we think that it is possible that Aphnaeini may be the earliest offshoot of Lycaeninae, and that their ancestor was the first lycaenine to enter Gondwana from Laurasia. In that case, it might be expected that the tribe would be represented in South America. Their absence is hard to explain satisfactorily. The tribe at present comprises primarily denizens of scrubland and savannah and one possible explanation of their absence is that the ancestral stock was not adapted to the forested regions where Africa and South America were last in contact. In any case, it seems most probable that their acquisition of *Morpho* (flute)-type scales arose independently.

III. Origin of *Morpho* (flute)-type scales

At first sight, an independent origin seems most likely for the *Morpho* (flute)-type scales. The change from an undifferentiated scale is not very great, involving merely a closer approach of the ridges to one another and an enlargement of the flutes, followed by their inclination from the vertical. For example, the orange scales of *Poecilmitis chrysaor* (Figs 2C, D), in which the flutes are at 90° to the plane of the scale, require only a little development to transform them into *Morpho* (flute)-like scales similar to the co-tribal *Spindasis* species. By contrast, the evolution of *Urania*-type scales involves the complete conversion of the trabeculae into a series of laminae held apart by small bead-like separators. Transmutation of *Urania*- to *Morpho*-type involves not only loss of the laminae but also recreation of the trabeculae. Nevertheless, assuming that we are correct in thinking that *Urania*-type scales came first, the discovery of apparently intermediate scales in representatives of the genera *Chliaria* and *Siderus* makes it desirable to examine whether and how such a transmutation

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might be possible.

A possible transition of *Urania*-type to *Morpho*-type might take the following path. The first step could be the reduction of the multilayers to a single layer, giving rise to a taller ridge in which the upright flutes are more pronounced. This step is seen in the pale blue scales of *Chliaria othona*. The next step might be the loss of the single pepper-pot layer, as seen in the pigmented scale of *C. othona* from the dark apical area of the forewing. The ridges and their spacing differ very little from the blue scale, with the flutes remaining upright so that the violet colour only becomes visible near grazing incidence. The next steps would be the inclination of the flutes towards the horizontal, *i. e.* parallel to the reverse surface, combined with a closer approach of the ridges to one another. At first the inclination would be slight, as in *Rapala manea*, *Spindasis nipalicus* and *S. syama*, so that the iridescent blue only becomes visible when the wings are viewed at an oblique angle. The tilting is envisaged to increase gradually, as in *Hypolycaena erylus*, and *Sithon nedimond*, to culminate in the final stage, as in *Artipe eryx*, where the flutes are parallel to the lower lamella over much of the scale, and the iridescent blue is strongest when the wings are viewed "head-on".

If we are wrong in thinking that *Urania*-type scales occurred first in Lycaenidae, then the reverse process, *Morpho*-type to *Urania*-type, could equally well have taken place.

Conclusions

The discovery of *Morpho* (flute)-type scales in addition to the *Urania* (pepper-pot)-type scale morphology in the Lycaenidae adds significant new data to the study of this group. The distribution of these two scale microstructures within the family suggests that scale morphology can make a limited contribution to the clarification of the phylogenetics and taxonomy of butterflies in general. In this respect, it is generally accepted that Lycaenidae, Riodinidae and Nymphalidae share a common ancestor. The latter two families, so far as we know, possess only *Morpho* (scute)-type structural scales. In view of the results reported here for the Lycaenidae, and by Ghiradella (1985), for the Papilionidae, comparative investigations of scale morphology in Riodinidae and Nymphalidae might be fruitful.

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摘　　要

シジミチョウ科の鱗粉の微細構造と系統発生学的意味合い (R. J. D. Tilley • J. N. Eliot)

シジミチョウ科47種とシジミタテハ科7種について，緑，青，紫といった光沢を発する鱗粉の微細構造を調べた．構造色による虹様光沢には，*Urania* (ツバメガ) 型と *Morpho* (モルフォチョウ) 型

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が知られる．調べたシジミチョウのほとんどは，鱗粉表層部の多重層による *Urania* 型であったが，予期せぬことに，Lycaeninae (シジミチョウ亜科) の Aphnaeini (キマダラルリツバメ族) と，Eumaeini (カラスシジミ族) の中の Deudorigina (トラフシジミ亜族) と Hypolycaenina のいくつかの種で *Morpho* 型が観察された．シジミチョウ科の *Urania* 型は，Eliot (1973) によって "pepper-pot" (胡椒入れ) 型と名付けられたように，多重層に多かれ少なかれ穴の開いたやや複雑な微細構造を示すものが大部分であった．一方，シジミチョウ科の *Morpho* 型は，鱗粉表面の縦隆起 (ridge) の側面に生じる縦溝 (flute) の作用によるもので (*Morpho* (flute) 型)，縦隆起側面の scute によるシジミタテハ科，タテハチョウ科，シロチョウ科，アゲハチョウ科の *Morpho* (scute) 型とは全く異なっていた．

系統や分類の分野では，鱗粉の形態は従来あまり用いられて来なかった．これは，類似した型のものが複数の科にまたがって現われるからである．しかし，シジミチョウ科の光沢鱗のほとんどが，蝶の他の科では見られない *Urania* (pepper-pot) 型であることや，今回見つかった *Morpho* 型が flute 型であることは重要と考えられる．*Morpho* (flute) 型は，例外的にアカエリトリバネアゲハの翅表の緑色鱗と裏面の青色鱗に認められる以外は，シジミチョウ科に特徴的と思われる．また，シジミタテハ科では，シジミチョウ科に現われる様々な型のどの 1 つも見られず，特に構造色鱗はタテハチョウ科で報告されているものと同じであった．シジミタテハ科については，従来，シジミチョウ科の 1 亜科として他のシジミチョウと姉妹群を成すという考えや，シジミチョウ科の姉妹群となる独立した科，またはタテハチョウ科の姉妹群となる科とする意見が提出されてきた．今回の観察は，シジミタテハ科とタテハチョウ科を姉妹群とする見解を支援する新しい情報を提供する．

シジミチョウ科の中で，どちらの型の鱗粉が最初に獲得されたかを解くには，南米のシジミチョウ科を考慮する必要がある．南米は，北米経由のアンデス産のいくつかの Polyommatina (ヒメシジミ亜族) を別とすれば，亜族 Eumaeina のみが分布する．シジミチョウ科の起源は白亜期初期におけるローラシアのユーラシア域と信じられるが，ゴンドワナ大陸のアフリカ/南米陸塊へのシジミチョウ科の侵入は "ジブラルタル・ルート" であったろうとされ，白亜期中期前後の 2 つの大陸の分離時期には祖先的 Eumaeini のみが存在したとするのが論理的である (そうでなければ，今の南米には Eumaeini 以外のシジミチョウ科も分布する筈である)．亜族 Eumaeina では *Urania* 型の鱗粉のみが見られることから，シジミチョウ科の構造色鱗の起源は *Urania* 型で，*Morpho* 型は 2 つの大陸の分離後アフリカで進化したと推測できる．*Urania* 型が先に現われたとする根拠は，それが Poritiinae (キララシジミ亜科) に見られることにもある．一般にシジミチョウ科の初期の分岐は，Poritiinae, Miletinae (アシナガシジミ亜科), Curetinae (ウラギンシジミ亜科) へと続く枝からのシジミチョウ亜科の分離を導いたと考えられるので，*Urania* 型鱗粉はこの非常に早い段階で既に存在していたと推定される．

Morpho (flute) 型を有する 3 つのグループの内，亜族 Deudorigina と Hypolycaenina は，♂交尾器や翅脈から見て互いに近縁であり，また亜族 Eumaeina とも近縁である．Deudorigina と Hypolycaenina はアフリカに分布の中心があり，恐らくインド大陸がアジアに衝突した後，東洋区や旧北区の東南縁に広がった．これは，*Morpho* (flute) 型がアフリカ大陸の分離後にアフリカで生じた考えをうまく説明できる．問題は残る 1 つの Aphnaeini 族である．この族はシジミチョウ亜科で最も早く分岐したグループと考えられ，ローラシアからゴンドワナ大陸に最初に入ったシジミチョウと考えられるが，そうであれば，この族が南米に産しないことは説明しづらい．この族の祖先が森林地域に適応できなかったというのがその説明になるかも知れないが，いずれにせよ，Aphnaeini 族での *Morpho* (flute) 型の獲得は独自に起こったと考えるのが最もありうるように思われる．

Morpho (flute) 型鱗粉は，未分化 (undifferentiated) 鱗と *Urania* 型鱗粉から別々に生じたように思われる．細部で高度に改変された *Urania* 型からの変形はやや想定しづらいかも知れないが，*Chliaria* 属や *Siderus* 属のいくつかの種では明らかに中間的な鱗粉が観察され，その変形過程の説明を可能とする．恐らく，多重層が単層になることで鱗粉表面の縦隆起 (ridge) が高くなり，直立した縦溝 (flute) も顕著となる．次いで単一の "pepper-pot" 層も失われ，縦隆起の間隔が狭まるとともに，縦溝の傾斜が起き，最終的には鱗粉の表層下面と平行になるところまで傾斜が進んだと考えられる．

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